

Acoustical Behavior of the Menpachi, *Myripristis berndti*, in Hawaii¹

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ABSTRACT: The menpachi (*Myripristis berndti*) is found in aggregations inside caves and under ledges during the day in water more than 3 m deep. Diel tape recordings in these areas showed that the fish produced four types of sounds (knocks, growls, grunts, and staccatos), with no crepuscular peaks, from dawn to dusk. At night, when the fish scattered to feed, few sounds were detected.

A fifth sound was produced when fish were hand-held. The sound-producing mechanism was determined by a series of ablation experiments on hand-held fish. It consisted of a pair of bilateral muscles attached to the skull anteriorly and the air bladder, the first two dorsal ribs, and the cleithrum bone posteriorly.

Populations of 6-7 fish were maintained in the laboratory in large tanks with an artificial cave. They remained inside the cave during the day but swam actively throughout the tank at night. Brief chasing of a small fish by a larger, accompanied by knocking sounds, was frequently observed. Growl sounds were produced during more intense aggressive interactions between two fish of about the same size. There was no evidence of territoriality by members of any population.

Few grunt or staccato sounds were produced when various species of nonpredatory fish were introduced among laboratory populations. Many of these sounds were elicited when moray eels were introduced.

Sound playbacks to four populations from one of two speakers on either side of the cave elicited different responses depending on the sound tested. All fish immediately turned to and moved toward the experimental speaker when grunt or staccato sounds were played. Some fish briefly turned to the experimental speaker when knocks were emitted but none moved to the source. There was no detectable change in behavior when background noise was played back.

Three fish tested in an aktograph showed increases in locomotory activity at night which corresponded with periods of nocturnal scattering and feeding in field populations.

The acoustical system of the menpachi is compared with that of the longspine squirrelfish, *Holocentrus rufus*, an Atlantic species.

THE "MENPACHI" consist of four species of economically important fishes in the Hawaiian area. Although their habits are well known to trap- and spearfishermen, there have been few published studies on their ecology and none on their acoustical behavior. In this report the behavior correlated with or stimuli eliciting four types of sounds (grunts, staccato, knocks, and growls) produced by *Myripristis berndti* (Jordan and Evermann) are described. A fifth

sound, produced when fish were hand-held, was physically analyzed in conjunction with experiments to determine the sound-producing mechanism. Diel patterns of locomotory and feeding activity in nonreproductive groups of *M. berndti*, and their relationship to sound production were determined by field and laboratory observations. Experiments were carried out to determine the response of laboratory populations to playbacks of their own sounds and to other fish species commonly associated with them in their coral reef community.

It has been known for many years that several species of squirrelfishes (family Holo-

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centridae) produce sounds. Studies to date have been made on two species in the genus *Holocentrus*. Fish (1948) first reported sound production in the group. Moulton (1958) studied *H. ascensionis* in Bimini and described two types of sounds produced in the field, a single sound (the grunt) and one composed of several thumplike sounds produced in a series (the staccato). Winn, Marshall, and Hazlett (1964) were the first to study the significance of these sounds experimentally. They found that the nonreproductive social organization of *H. rufus*, which produced the same types of sounds as *H. ascensionis*, was territorial. When a conspecific individual entered the territory of another squirrelfish, the resident produced many grunt sounds and rarely staccatos, sometimes accompanied by fin erection, nipping, and lateral displays in which the two fish moved parallel to each other. Intruders of other species elicited both staccatos and grunts, but more staccatos were produced toward larger fish or a potential predator, such as a moray eel. Laboratory populations were maintained in large tanks and each fish defended a territory consisting of the inside of a large can, open at one end, and the area immediately before the opening. When staccato sounds were played back to these populations from one of two speakers on each side of the tank, the fish at first retreated into their cans. Some then swam to the sound source, while others turned their heads toward the speaker from just outside the can, indicating that the fish were probably able to localize the source of sound. Diel recording showed that more sounds were produced during the day than at night, when the fish were active and feeding. Peaks in sound production occurred at dawn and dusk. It was hypothesized that the peaks were caused by movements of nocturnal and diurnal species into and out of the reef and through the territories of squirrelfishes under conditions of reduced light intensity.

Moulton (1958) stated that contractions of the body wall musculature associated with the first three ribs and the air bladder were responsible for sound production in *H. ascensionis*. In a series of ablation experiments, Winn and Marshall (1963) showed that the muscles involved in sound production were bilateral and attached to the posterior part of

the skull, the air bladder, and the first two dorsal ribs in *H. rufus*. Removal of one muscle reduced the intensity of sounds produced by hand-held specimens, but did not significantly change sound duration or number of pulses per sound, indicating that the two muscles contracted simultaneously to produce each sound. Gainer, Kusano, and Mathewson (1965) studied the electrophysiological and mechanical properties of the sound-producing muscle in the same species. The muscle was capable of contracting at a frequency of 100/second with no mechanical summation, while fast white muscle from the same fish showed considerable summation at 50/second.

Myripristis is the second largest genus in the family. These fish live in schools and move over the reef more than do members of the genus *Holocentrus* (Herald, 1961), which are solitary-territorial. Other reports indicate that the schools remain in caves or under ledges during the day and scatter to feed at night (Hobson, 1965). The presence of sand-dwelling annelids in the stomachs of *M. berndti* from the Marshall Islands indicated that the fish move to open areas, away from the reef during nocturnal feeding (Hiatt and Strasburg, 1960).

There have been no published studies on the acoustical behavior of any species in this genus. Nelson (1955) described the antero-bilateral projections of the air bladder which, in *M. argyromus*, completely covered the auditory bullae and were thus more extensively modified, presumably for an auditory function, than in *H. ascensionis* and *H. rufus*.

MATERIALS AND METHODS

All observations and experiments were carried out at Oahu, Hawaii, from February to July 1965. Most of the field observations were made in Pokai Bay, Waianae, in water 3–9 m deep. The study area spanned a 1-km distance along the coast. Several other schools were observed in similar habitats offshore at Black Point and Ilikai Harbor. The topographic features of the habitats and estimates of school size in number of fish were recorded with the aid of an underwater flashlight and drawing pad or were photographed directly with a Nikonos underwater camera.

All tape recordings were made with an Uher 4000-S Report recorder and an Atlantic Research Corp. hydrophone (Model LC-57). Field recordings were carried out by securing a boat with three anchors over the reef area containing a school of fish. The hydrophone was placed inside a cave or under a ledge within 1 m of the fish and was secured with a weight. A small air-filled bottle was attached to the hydrophone cable about 1 m from the water surface to keep the cable taut and prevent entanglement in the reef. Field recordings were made at tape speeds of 2.3 cm/sec ($\frac{1}{8}$ i.p.s.); laboratory recordings were made at 9.5 cm/sec ($3\frac{3}{4}$ i.p.s.).

Specimens 12–20 cm in total length were caught by hook and line or in traps and brought into the laboratory for study under more controlled conditions. They were established in groups of 6–7 fish in 756-liter fiberglass tanks with a plexiglas front, in which a "cave" was constructed with two building blocks covered with a piece of masonite (Fig. 1). Holes in the blocks allowed the fish to enter and leave through the side as well as through the front of the cave. A continuous flow of fresh sea

water circulated through the tank at temperatures between 21° and 23° C. The hydrophone was suspended in front of the cave to record sounds. Behavior correlated with sound production was described immediately after recording the sounds.

Sound playbacks were carried out. One underwater speaker (University MM-2L) was placed on each side of the cave. The sounds used for playbacks were all recorded from previous populations of *M. berndti*. They were played through one of the speakers from a continuous loop of tape on a Crown tape recorder (Model CR-25) which repeated the entire playback every 11 seconds. The response of four populations to grunt, staccato, and knock sounds was determined. Each type of sound was played back once in a random order to each group of fish and at levels comparable to those emitted by the fish. The number of fish on the left or right side of the tank was determined every 15 seconds of a 5-minute period with sounds played back during minutes 2 and 4 from one speaker, selected randomly. Recordings were made during the entire 5-minute period to monitor playbacks and record any sounds produced by the fish. One observer (the recorder) noted the position of the fish in the tank. Another, shielded from both the fish and the recorder, turned the sound on and off through one of the two speakers. The recorder had no prior knowledge of which speaker was being used during the test although the response of fish to certain sounds enabled him to determine the experimental speaker with 100% accuracy.

Various species of fish commonly associated with *M. berndti* in the field were introduced in a random order to seven individual populations. These were: *Myripristis berndti*, *M. argyromus*, *Holocentrus xantherythrus*, *Priacanthus meeki*, *Parupeneus porphyreus*, and *Gymnothorax undulatus*. The type and number of sounds produced by the populations were recorded for a 1-minute period before and during the introduction.

Patterns of locomotory activity were determined for three fish, one for 24, one for 56, and one for 72 hours. The fish were placed singly in a large doughnut-shaped chamber 7.6 cm wide, 9.5 cm deep, and with a mean swimming circumference of 87.6 cm. Fresh aerated

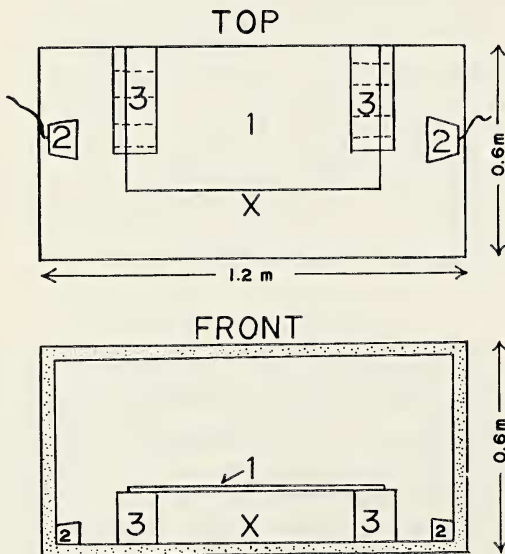


FIG. 1. Top and front views of tank in which laboratory populations were maintained, showing outside dimensions. 1, Roof of cave; 2, underwater speakers used in sound playbacks; 3, building blocks with two holes through which fish could enter and leave the cave through the side as well as by the front opening; X, position of hydrophone.

sea water circulated through the chamber at all times. Two Pflueger Fish Finders (Enterprise Manufacturing Co.), placed 180° apart and positioned to face toward the center of the chamber, were used to detect the movement of the fish. The fish finder emits an 800-kc signal as a narrow beam across the chamber. The reflected signal is identical to the emitted one when no moving object is present and, when the signals are compared (heterodyned) in the receiver, they cancel out. Movement of a fish past the fish finder shifted the frequency of the reflected signal and caused a deflection on the chart of a Rustrak event recorder (Model 92). The chamber was placed in a small room within 1 m of a large window, so that the fish was exposed to normal changes in the daily light cycle. For further details concerning the apparatus, see Muir et al. (1965).

A series of ablation experiments was carried out to determine the sound-producing mechanism. All fish produced grunts when hand-held by the caudal peduncle. Sounds of normal hand-held fish were recorded, followed by recordings of the same fish (record level on tape recorder left constant) after removal of the following: one or both sound-producing muscles; other associated muscles and bones; the gas from the swim bladder. All fish were held about 7.5 cm from the hydrophone. Operated fish were anesthetized with MS-222. A few muscle potentials were recorded from the sound producing muscle of two fish with a Tektronix Low Level Amplifier (Type RM-122) and oscilloscope (RM-504) and were photographed with a Grass camera (Model C-4). The sound duration, number of pulses, and interpulse intervals were measured by photographing the recorded sounds from a Fairchild oscilloscope (Model 701) with the Grass camera, at film speeds of 100–500 mm/sec.

The effect of operations on the intensity of sounds was determined. A General Radio Co. Impact-Noise Analyzer (Type 1556-B) was connected to the output of the tape recorder and a peak sound pressure value was determined for a normal fish. The peak sound pressure of the same fish after the operation was also obtained. The peak value for the normal sound was considered as 0 decibel, while the value for the operated fish was considered as

positive db (if the value exceeded that of the normal fish) or negative db (if the value was less). Relative sound pressures at various octave band frequencies were also measured. The output of a General Radio Co. Octave Band Noise Analyzer (Type 1558-A) was connected to the input of the impact analyzer. A sine wave of 400 cps was applied to the input of the octave band analyzer when set in the "all pass" position, and with the preamplifier in the 20 Kcs weighting (essentially flat response from 20 cps to 40 Kcs). The impact analyzer was then calibrated to give a peak value 3 db higher than the root mean square value shown by the octave band analyzer for the sine wave. After calibration, the fish sounds from the tape recorder were applied to the input of the octave band analyzer and readings were determined from the impact analyzer. The loudest of the first five sounds produced by a normal fish was measured and considered as 0 db. All sound pressures in various octave band frequencies of the first five sounds produced before and after operations on this fish were compared with the 0 db value. The sound pressures of all filtered signals were always less than the 0 db value. The reduction was measured and expressed in decibels. All sound pressures obtained from the impact analyzer were relative to 0.0002 microbar.

RESULTS

The Sound-Producing Mechanism

Sounds produced by hand-held specimens were accompanied by vibrations which could be felt along an area extending from the dorso-lateral region of the skull to the side of the body just lateral to the air bladder. The most intense contractions were in the dorsal region behind the eye. Removal of some of the superficial muscles, opercula, and part of the suprascapular bone revealed a band of muscle slightly yellow in appearance, which could be observed to contract synchronously with the production of sound. The muscle was attached to the posterior part of the skull, just above the eye, and passed over the anterior lobes of the air bladder to its insertion point above the area where the main body of the air bladder gives rise to the lobes (Fig. 2). At its insertion, the muscle was attached medially to the first two dorsal ribs and

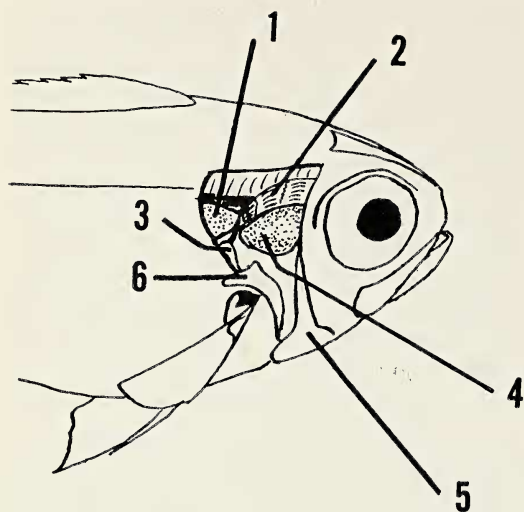


FIG. 2. Anatomy of the sound-producing mechanism and surrounding bones in *Myripristis berndti*. 1, Main body of swim bladder; 2, sound-producing muscle; 3, dorsal portion of cleithrum bone with tendon attached to sound-producing muscle; 4, anterior lobe of swim bladder; 5, preoperculum; 6, scapula.

the air bladder. A small tendon connected the muscle to the cleithrum bone laterally. Another small, flat muscle (not shown in the figure) attached to the skull and ran between the sound-producing muscle and the anterior lobe of the air bladder, to the operculum. This muscle was routinely cut during ablation experiments, with no apparent effect on sound production. The sound-producing muscle was highly vascularized and appeared to be composed of three distinct myomeres.

Removal of one sound-producing muscle resulted in a relative decrease of 2–7 db in operated fish, when compared with their own normal sounds (Table 1). Sound pressures were reduced in all octave bands but were greatest in the 75–150 cps band. Normal sounds contained frequencies below 75 cps to under 4,800 cps, with most energy between 300–600 cps. Oscillographs of these sounds are shown in Figure 3.

The temporal patterns of the pulses within these sounds are shown in Table 2. Normal fish produced sounds composed of 7–10 pulses (mean, 8.2). Operated fish showed more variability in pulse range (6–11), and a mean

value of 9.04 pulses per sound. Increases in number of pulses were correlated with increases in sound duration. Interpulse intervals were variable, but in most sounds the intervals between the penultimate and the last pulse were greater than between other pulses. A few muscle potentials recorded from two fish were composed of 6–8 spikes (Fig. 3). The interspike intervals and total duration for a series of spikes were comparable to values for interpulse and total-duration measurements of sounds with the same number of pulses.

The effect of removing the superficial muscles and bones near the sound-producing muscle is shown in Table 3 and Figure 3. The peak pressure of sounds produced by operated fish, when compared with pressures of their own sounds before the operation, increased in one fish, decreased in two, and remained the same in two fish.

Five fish in which both sound-producing muscles were removed produced no audible sounds.

The role of the air bladder in sound production was determined by replacing the gas in the bladder with sea water. Five fish, in which a small hole had been punctured in the lobe of the air bladder with a syringe, continued to produce sounds at intensities comparable to their own normal sounds (mean peak sound pressure = 1.1 db above normal fish). Only a few bubbles of gas escaped through the puncture. When the puncture was held open the intensity of the sounds decreased as gas escaped until finally, when the air bladder was completely filled with water, no audible sounds were produced although the muscles could still be felt to contract. The presence of only a small bubble of gas in the bladder resulted in production of sounds of very low intensity.

Field Observations and Diel Recordings

At least 20 different schools of menpachi were found in the Pokai Bay area. In all cases, these were mixed assemblages of *M. berndti* and *M. argyromus*, from 13 to 23 cm in total length. In shallower waters, *M. argyromus* predominated. Both species were found to produce the same types of sounds and to have similar nocturnal-diurnal activity patterns in

TABLE 1
 PEAK PRESSURE CHANGE AND RANGE OF PRESSURES IN OCTAVE BANDS OF FISH SOUNDS BEFORE (NORMAL) AND AFTER (OPERATED) REMOVAL OF ONE SOUND-PRODUCING MUSCLE¹

CONDITION	PEAK PRESSURE CHANGE IN OPERATED FISH	RANGE OF OCTAVE BAND SOUND PRESSURES IN DB							
		75-150	150-300	300-600	600-1200	1200-2400	2400-4800		
Normal		19-25	14	4-6	11-12	29-32	39		
Operated	-7 db	36-38	22-24	11-13	14-16	31-33	—*		
Normal		29-30	13-14	3-5	9-11	24-28	—		
Operated	-4 db	31	17-19	9-11	10-12	27-30	—		
Normal		26-29	14-17	3-6	9-12	25-29	—		
Operated	-4 db	32-34	17-20	7-9	11-14	22-23	—		
Normal		28-30	15-17	4-6	9-10	20-22	—		
Operated	-5 db	35	20-22	9-10	13-14	22-23	—		
Normal		28-30	14-15	4-5	7-9	22-23	—		
Operated	-2 db	31-34	17-19	7-9	7-8	24-26	—		

¹ Values represent db below total sound energy, so that the smallest reductions represent the octave bands of greatest amplitude.

* Sound pressures below ambient level.

TABLE 2
 TOTAL DURATION, NUMBER OF PULSES, AND INTERPULSE INTERVALS OF HAND-HELD SOUNDS PRODUCED BY
 FIVE FISH BEFORE (NORMAL) AND AFTER (OPERATED) REMOVAL OF ONE SOUND-PRODUCING MUSCLE

NO. OF SOUNDS	NO. OF PULSES	AVG AND RANGE OF SOUND DURATION (MSEC)	AVERAGE AND RANGE OF TIME (MSEC) BETWEEN PULSES												
			1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12		
Normal Fish															
6	7	88.5 80-92	8.7 8-10	14.8 10-22	10.7 8-14	11.0 8-14	11.8 8-13	13.0 9-19							
11	8	94.4 89-104	9.4 8-11	9.7 8-12	11.0 9-13	10.0 8-12	11.2 10-12	11.3 10-13	14.6 11-19						
6	9	103.0 100-106	9.2 8-10	9.7 8-11	10.5 10-12	10.2 10-11	10.2 9-11	10.7 10-12	10.7 10-12	14.7 12-18					
2	10	116.0 114-118	10.0 10	9.0 8-10	11.0 10-12	10.0 10	10.0 10	10.5 10-11	10.5 10-11	11.0 10-12	14.0 13-15				
Operated Fish															
1	6	78.0	10.0	11.0	12.0	12.0	22.0								
2	7	93.0 76-110	9.5 9-10	13.0 10-16	9.5 9-10	14.0 10-18	10.0 10	17.5 13-22							
7	8	104.0 90-160	10.4 9-12	15.0 10-27	10.0 9-11	13.6 10-27	10.3 9-12	15.6 10-42	11.9 10-13						
6	9	101.5 94-101	10.2 8-12	10.3 9-12	10.2 10-11	10.0 9-11	10.7 9-15	10.3 10-12	10.8 10-13	13.2 10-17					
4	10	113.3 108-128	10.8 10-13	10.3 10-11	10.0 9-11	10.0 10	10.0 10	10.0 10	10.0 9-11	14.3 12-20					
4	11	114.0 106-124	9.5 8-10	9.5 8-10	9.3 8-10	9.3 8-10	9.5 8-10	9.8 9-10	10.0 9-11	10.3 9-12	11.0 10-12	12.8 11-14			
1	12	125.0	10.0	10.0	10.0	10.0	12.0	10.0	10.0	11.0	10.0	12.0	14.0		

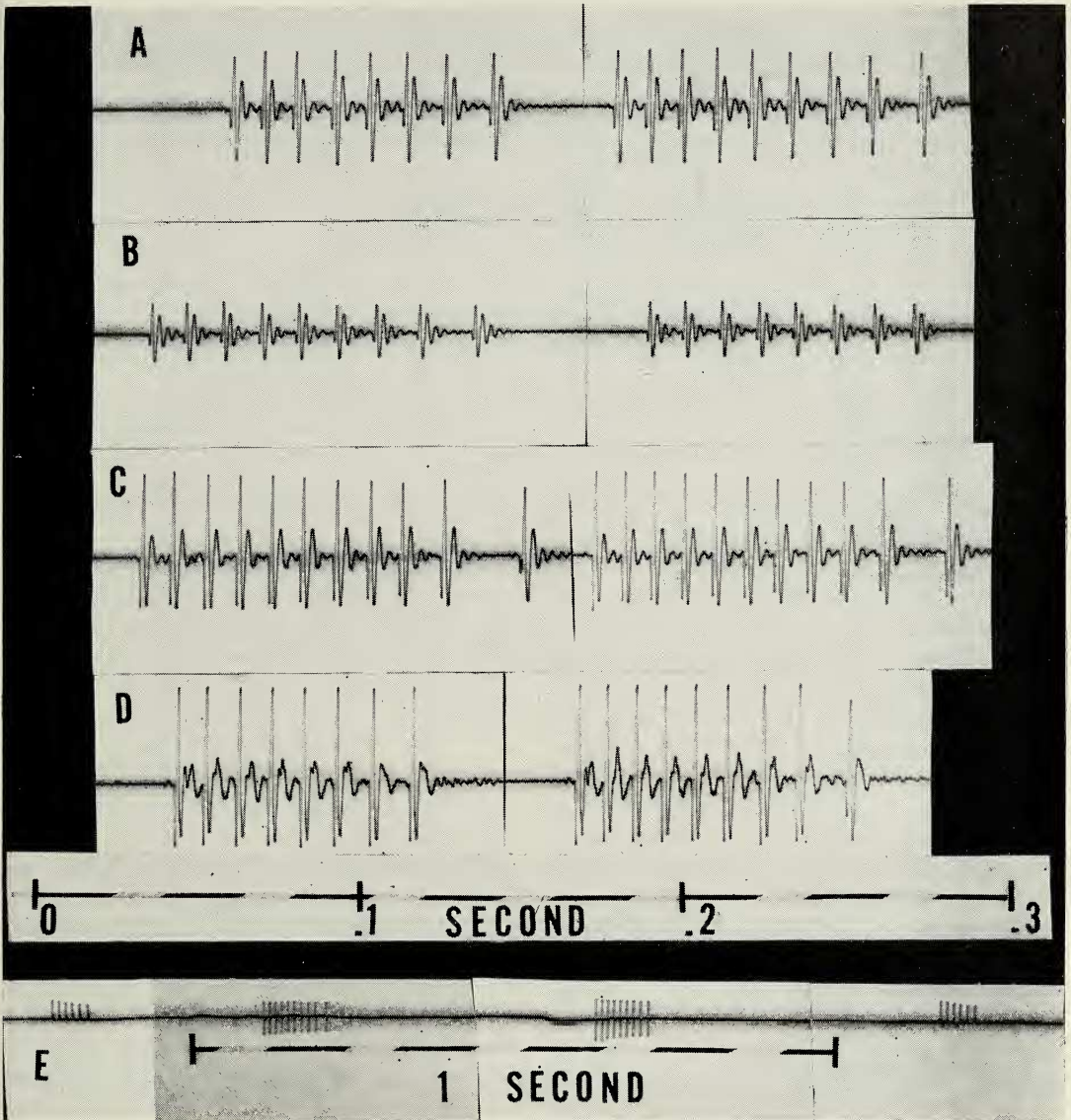


FIG. 3. Oscillographs of grunt sounds and muscle potentials from hand-held *Myripristis berndii*. *A*, Two sounds from a normal fish; *B*, two sounds from the same fish after one sound-producing muscle has been removed. Note decrease in intensity. *C*, Two sounds from another normal fish; *D*, two sounds from the same fish after superficial muscles and bones over one sound-producing muscle have been removed; *E*, muscle potentials corresponding to four hand-held sounds recorded from two other fish.

the field. The schools varied in size from 8 to more than 100 fish, depending upon the space in the area in which they were located. Fish were found in one of three different habitats at depths to 9 m: under ledges which extended 1–6 m deep and 3–20 m long, raised 0.2–1.5 m off the bottom; in caves with openings 1–3 m in diameter and variable inside

dimensions; and in recesses within mounds of glomerate coral located within 1–3 m from the bottom. The same types of habitats were occupied by several populations found offshore at Black Point and the Ilikai Harbor.

During 26 days of daytime field observations (between 0800 and 1730 hours) scattered over a 3-month period the presence of schools in

TABLE 3

PEAK PRESSURE CHANGE AND RANGE OF PRESSURES IN OCTAVE BANDS OF FISH SOUNDS BEFORE (NORMAL) AND AFTER (OPERATED) REMOVAL OF THE MUSCLES AND BONES OVER THE SOUND-PRODUCING MUSCLE

CONDITION	PEAK PRESSURE CHANGE IN OPERATED FISH	RANGE OF OCTAVE BAND SOUND PRESSURES IN DB					
		75-150	150-300	300-600	600-1200	1200-2400	2400-4800
Normal		16-18	3-7	5-6	1-4	16-19	31-34
Operated	+2 db	21-24	8-9	4-6	6	19-20	33-36
Normal		23-26	11	4-5	6-7	19	32-33
Operated	-1 db	29-30	14-15	6-7	10	21-22	36-41
Normal		23-36	8-12	5-8	5-8	17-20	33-35
Operated	0 db	25-27	11-12	6-7	5-6	17-19	30-34
Normal		25-27	13-14	7-8	5	19	21-22
Operated	-1 db	27-28	15-16	8-11	6-7	15-17	32-33
Normal		29-31	14	6-7	5	16	31-32
Operated	0 db	28-30	14	7-9	4-8	16-19	30-32

these habitats was always observed. None of the fish were ever seen swimming in open water during the day. Associated with the schools of menpachi were groups of other squirrelfish (*H. ensifer*, *H. xantherythrus*, and *H. spinifer*—usually a single specimen), aweoweo (*Priacanthus cruentatus* and *P. meeki*), moray eels (*Gymnothorax* sp.), cardinal fish (*Apogon* sp.) and pipefish (*Syngnathus* sp.). Various other diurnal species of reef fishes were observed to enter and leave caves and ledges. The frequent visits of large schools of goatfish (*Parupeneus* sp.) did not result in production of staccato and grunt sounds when the entrances coincided with diel recordings.

It was not possible to carry out detailed observations on the behavior of menpachi in these areas, even with SCUBA gear. A diver's presence resulted in retreat by the fish into darker and less accessible areas, accompanied by the production of many staccato and grunt sounds. Only a few fish briefly investigated the diver within the first minute or two after he appeared. When the caves or ledges were too shallow for backward retreat, the school scattered to either side or rushed quickly back and forth within the confines of the area.

Many menpachi (both *M. berndti* and *M. argyromus*) were caught with hook and line. The bait was kept off the bottom, just outside the ledge or cave opening. No fish were ever caught or took bait during the day. All 57 fish caught by fishing during the study period were captured between 1930 and 2030 hours, al-

though on some nights fishing continued until midnight.

Tap recordings in the field were carried out in four different areas of Pokai Bay, three for a 24-hour and one for a 9-hour period. The results are shown in Table 4. Four types of sounds were recorded: (1) staccatos, (2) grunts, (3) a series of knocking sounds variable both in intervals between consecutive knocks and in number of knocks in a series, and (4) growls, consisting of a rapid series of sounds lasting from 1 to 4 seconds. Oscillographs of these types of sounds recorded from laboratory populations are shown in Figure 4. Only a few of these kinds of sounds were produced after sunset and before sunrise. Knocks were the most frequently recorded of all sounds, with no obvious peaks in rate of production after an initial increase following dawn. In one 24-hour recording (April 28-29), there was a peak in staccato and grunt sounds at dusk.

General Behavior of Laboratory Populations

Laboratory populations confined their daytime movements to slow swimming inside the cave, with occasional chasing of one fish by another. Individual fish occasionally swam outside of the cave for a few seconds. When lights were turned off at night, the movements of fish could still be detected in the available ambient light. Within 5 minutes, the fish were swimming rapidly around the tank above the cave. Several populations all produced sounds in the laboratory at night when recordings were

TABLE 4
 DIEL PATTERNS OF SOUND PRODUCTION (FIELD) AND LOCOMOTORY ACTIVITY (LABORATORY) IN *Myripristis berndti*

ACTIVITY RECORDED	DATE	TIME*																								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
Sound production (four schools)	4/28	Stac.	0	0	0	0	0	0	0	0	0	0	18	13	4	6	1	0	2	28	1	0	0	0	0	0
		Grnt.	0	0	0	0	0	1	0	0	0	1	8	11	9	16	14	1	5	20	1	0	0	0	0	0
		Knck.	0	0	0	0	6	19	12	12	14	21	16	30	37	35	36	16	21	25	39	0	2	0	1	0
		Grwl.	0	0	0	0	1	1	3	1	2	8	3	9	4	5	9	3	1	2	13	4	0	0	0	0
	6/6	Stac.	0	0	0	0	0	1	0	3	0	11	17	6	5	0	0	1	1	4	0	0	0	0	0	
		Grnt.	0	0	0	0	0	0	0	0	4	1	1	4	0	0	0	0	0	1	0	0	0	0	0	
		Knck.	0	0	0	2	26	34	64	22	29	39	73	69	38	55	55	35	23	25	26	1	0	0	0	
		Grwl.	0	0	0	1	13	7	8	7	3	11	8	7	15	13	11	8	10	8	5	0	0	0	0	
	6/23	Stac.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	0	0	0	0	0		
		Grnt.	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0		
		Knck.	0	0	1	7	31	27	28	3	13	12	28	39	26	31	28	19	36	38	22	2	2	0	1	
		Grwl.	0	0	0	0	5	1	2	3	3	6	5	2	2	2	4	1	8	1	4	0	0	0	0	
	7/18	Stac.										4	3	2	8	4	0	0	1	0						
		Grnt.										4	10	6	5	9	2	3	6	0						
		Knck.										28	36	27	22	25	28	37	30	4						
		Grwl.										1	10	0	3	3	6	4	3	0						
Locomotory activity (three fish)	2/23	Fish 1	65	71	58	80	69	39	34	0	0	0	0	0	0	0	0	0	0	29	21	32	55	54	54	
		Fish 2	31	27	44	62	44	75	25	17	4	3	2	6	1	6	2	0	0	0	14	16	17	17	29	18
		Fish 3	15	15	9	18	19	25	6	10	10	17	6	3	6	5	8	9	11	10	22	40	17	12	28	69
	4/15	Fish 1	93	85	94	40	26	28	17	9	9	1	1	1	0	1	1	0	4	5	54	68	54			
		Fish 2	23	27	17	29	38	37	22	15	8	6	6	10	7	6	9	0	2	3	17	17	22	35	51	60
		Fish 3	53	33	65	59	61	28	15	35	27	20	17	30	22	18	17	13	11	8	25	51	39	49	62	36
		36	55	61	59	32	5	8	6																	

* Sunrise and sunset, July 1, 1965, at Oahu, Hawaii, were 5:53 AM and 7:18 PM, respectively.

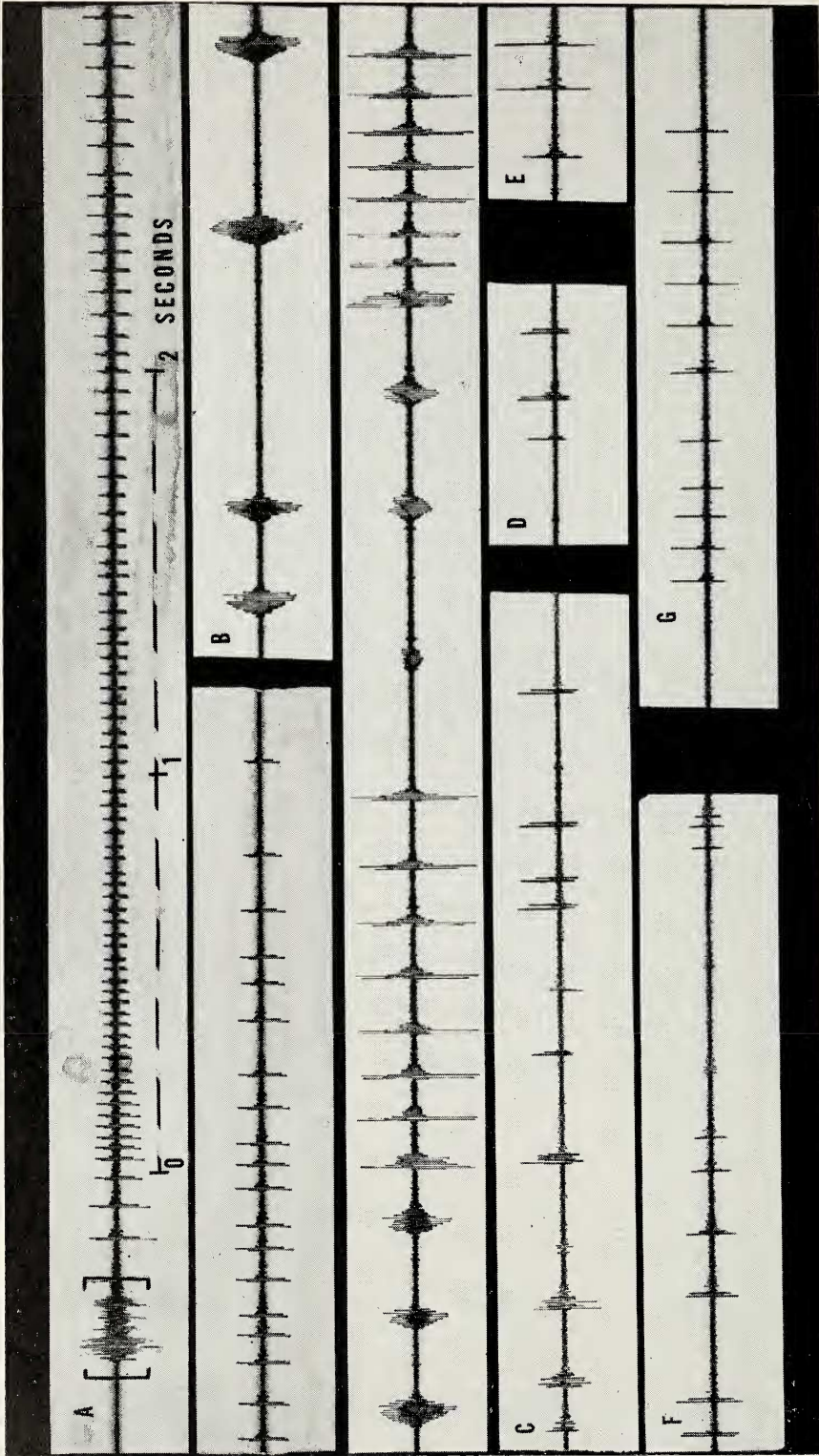


Fig. 4. Oscillographs of the four types of sounds produced by *Myripristis berrilli* in the field. A, growl, preceded by nipping sounds (between brackets) extending through upper line to half of line 2; B, seven grunts, followed by a staccato, 3 grunts, and another staccato. These sounds were produced by several fish. C-G, Five series of knock sounds produced during separate chasing episodes between pairs of fish.

made for 1–3-hour periods. The majority of the sounds produced were staccatos and grunts. Within 1 hour after the lights were turned off, all fish had assumed a pale red color, typical of individuals caught by fishing at night in the field.

Over 90% of all aggressive interactions consisted of brief chasing (1–3 seconds), usually accompanied by knock sounds. In a few cases physical contact between the aggressive and fleeing fish occurred. In five such instances the aggressive fish produced growl sounds just after nipping took place. On these occasions the attacked fish was about the same size as the aggressor and did not flee. The oscillograph in Figure 4 illustrates a typical growl sequence. The impact sound caused by body contact between two fish (within brackets) preceded the growl by several milliseconds. In four other observations, nipping did not occur but one aggressive fish dashed rapidly toward another, stopping just short of contact, and then produced the sound with his opercula slightly extended and mouth open. Aggressive behavior infrequently involved two fish which assumed parallel head-to-tail or head-to-head positions and slowly circled, beating their tails toward one another as they rotated, with opercula and mouth open but only the caudal fins spread. Knocking sounds were produced after one fish broke away and was chased by the other.

Usually it was not possible to determine which of the two fish produced the knock sounds during a chasing episode. In cases where the aggressor chased a fish from the front to the rear of the cave, both fish involved had their heads facing away and opening of the mouth and opercula, associated with sound production, could not be observed. When chasing across the front of the cave took place, the aggressive fish often stopped swimming near the hydrophone while the fleeing fish continued moving across the front or into the cave. In such cases, knock sounds increased in intensity as the aggressive fish approached the hydrophone while the fleeing fish moved several centimeters away. Often another faint series of knocking sounds occurred just after those of the attacking fish. These differed in pitch from those of the aggressive fish, indicating that the

chased fish might also be producing sounds. The general impression (not documented) was that more sounds were produced during longer periods of chasing. The majority of all aggressive interactions were initiated by a larger fish. A summary of the aggressive interactions of all populations is shown in Table 5.

Several of the smaller fish in three populations often adopted a characteristic posture when approached by an aggressive and larger fish. They elevated their heads while simultaneously tilting the ventral region toward the aggressor, exposing the pectoral area. In all cases, the aggressive fish broke off further contact and moved away. No staccato or grunt sounds were emitted during any aggressive interactions.

Locomotory Activity of Individual Fish

The number of pen deflections caused by single fish in the activity chamber were tallied per hour (Table 4). All fish showed consistently greater locomotory activity at night from 1900 to 0800 hours. Two fish showed continued activity through 0900. There were individual differences in the degree of daytime activity. There appeared to be a gradual rise to peak nocturnal activity during the first 3 hours after midnight.

Response to Introductions of Other Fish

The number of grunt and staccato sounds produced by populations 1 minute after other fish were introduced is shown in Table 6. In no case did these sounds precede the introduction. A few grunts and one staccato sound were produced by three populations to one *H. xantherythrus*, *P. meeki*, and *P. porphyreus*. In all cases, introduced fish immediately entered the cave. The greatest number of sounds was produced when a moray eel was presented. After entering the cave the eel immediately curled around one of the blocks with its head protruding inside and its tail outside the cave, and remained motionless. The majority of staccato sounds were produced when the eel appeared initially, but grunts were produced throughout the 1-minute period. Other behavior by menpachi in addition to sound production consisted of orientation to the eel's head and rapid swimming movements inside the

TABLE 5
SUMMARY OF AGGRESSIVE BEHAVIOR AND ASSOCIATED SOUND PRODUCTION IN EIGHT
LABORATORY POPULATIONS OF *Myripristis berndti*

POPULATION NUMBER	DURATION OF RECORDINGS	NUMBER OF AGGRESSIVE INTERACTIONS	AGGRESSIVE FISH		AGGRESSIVE BEHAVIOR WITH:		
			LARGER	SMALLER	KNOCKS	GROWLS	NO SOUNDS
1	2 hours	31	23	8	24	3	6
2	3 hours	28	(no data)		19	0	9
3	4 hours	95	82	13	77	0	18
4	3 hours	51	35	15	36	1	14
5	1 hour	9	(no data)		5	0	4
6	3 hours	34	26	8	19	1	14
7	3 hours	29	22	7	18	2	9
8	2 hours	20	19	1	9	2	11

cave. Some fish swam to the outside and briefly "investigated" the eel's tail, then dashed back into the cave. There was no indication of mobbing or aggressiveness toward the eel.

Response to Sound Playbacks

The number of fish on each side of the tank during sound-playback experiments is shown in Table 7. When sounds were not emitted, the fish distributed themselves throughout the area under the cave. In some instances the school tended to aggregate briefly on one or the other side of the cave during the experiment. This distribution continued when background noise inherent in all playbacks and knocking sounds were played back through one of the two speakers. A few fish briefly turned toward the experimental speaker during playbacks of knocking sounds. The response to a series of staccato and grunt sounds involved several behavior patterns. Initially, all fish immediately turned to the sound source. Within 5-10 seconds, they swam toward the speaker from

which the sounds were being emitted. From 2 to 5 fish moved out of the cave to this speaker and dashed rapidly back into the cave. There was a general increase in rate of swimming movements. No staccato or grunt sounds were produced by the populations during any playbacks. The response of one population to a single staccato sound, repeated every 11 seconds during minutes 2 and 4, was comparable to responses by other fish to a series of staccato sounds. A second population tested showed a less intense response although several individuals oriented and moved toward the sound source.

DISCUSSION

The ablation experiments demonstrated that sounds were produced by a pair of bilateral muscles and the air bladder. Removal of one of the muscles reduced sound pressures, particularly in the lower frequencies (75-150 cps). The interpulse intervals and mean number of pulses per sound were comparable in

TABLE 6
NUMBER OF GRUNT-STACCATO SOUNDS PRODUCED BY LABORATORY POPULATIONS OF
Myripristis berndti ONE MINUTE AFTER INTRODUCTIONS OF OTHER FISH

INTRODUCED FISH	POPULATION NUMBER						
	1	2	3	4	5	6	7
<i>Holocentrus xantherythrus</i>			0-0	0-0	0-0	0-0	3-1
<i>Priacanthus meeki</i>			6-0	7-0	0-0	0-0	0-0
<i>Myripristis berndti</i>			0-0	0-0	0-0	0-0	0-0
<i>Myripristis argyromus</i>			0-0	0-0	0-0	0-0	0-0
<i>Parupeneus porphyreus</i>			0-0	1-0	0-0	0-0	0-0
<i>Gymnothorax undulatus</i>	32-16	19-8	80-21	36-20	78-18	43-28	115-25

TABLE 7
RESPONSE OF FOUR POPULATIONS OF *Myripristis berndti* TO SOUND PLAYBACKS*

SOUND PLAYBACK	POPULATION NUMBER	SOUND OFF		SOUND ON	
		LEFT SIDE	RIGHT SIDE	CONTROL SIDE	EXPTL. SIDE
Background Noise	4	34	38	22	26
	5	38	46	29	27
	6	34	50	33	23
Many Staccato Sounds	7	35	37	22	26
	4	39	33	3	45
	5	39	45	11	45
Many Grunt Sounds	6	40	44	5	51
	7	27	45	3	45
	4	38	34	5	43
Single Series of Knocks	5	40	44	16	30
	6	54	30	4	52
	7	39	33	6	42
Single Staccato Sound	4	32	40	24	24
	5	37	47	24	32
	6	36	48	20	36
	7	33	39	7	41

* Values represent the total number of fish on each side of the tank every 15 seconds during minutes 1, 3, and 5 when no sounds were played back, and during minutes 2 and 4 when sounds were emitted from one (experimental) side of the cave.

sounds produced by fish before and after one muscle was removed. The two bilateral muscles must then contract synchronously. The same results were obtained by Winn and Marshall (1963) with *Holocentrus rufus*. It may be that synchronous contractions of muscles associated with sound production are universal, but more evidence is needed.

The relationship between the contraction rate of sound-producing muscles and the resultant frequencies of the sounds have been investigated electrophysiologically in a few fish. Potentials recorded from *Myripristis berndti* in this study and from *H. rufus* (Winn and Marshall, 1963) corresponded in temporal relations to the pulses of sounds made by hand-held fish. Similar results have been obtained in the pigfish, *Congiopodus leucopocilis* (Packard, 1960), the sculpin, *Myoxocephalus octodecimspinosus* (Barber and Mowbray, 1956), and for several species of catfishes (Tavolga, 1962). In squirrelfishes, handheld sounds contain frequencies from below 75 to about 4,800 cps. The fundamental frequency of the sounds (about 85 cps) is believed to be a direct translation of the muscle contraction frequency (Tavolga, 1964), while the higher frequencies are harmonics resulting

from resonance of the air bladder. It would be expected that removal of one sound-producing muscle would reduce the intensity of all frequencies, particularly the 75–150 cps octave band containing the fundamental, as was the case in *M. berndti*.

Replacing some of the gas in the air bladder with water reduced sound intensities, and when all the gas was removed, no audible sounds were produced. The results indicated that the air bladder acted as a resonator in the production of sounds. Similar results were obtained with *H. rufus* (Winn and Marshall, 1963) and other fishes in which an air bladder-muscle mechanism was involved in sound production (Tower, 1908; Hazlett and Winn, 1962).

Field observations during the day, 24-hour tape recordings, the behavior of populations in laboratory tanks, and locomotory patterns of single fish in the activity chamber lead to the following conclusions. Schools of menpachi congregate in areas of suitable cover during the day. Their presence can be detected during these times by the production of four distinct types of sounds. Fish can be caught by hook and line for a brief period after sunset (1930–2030 hours) as they emerge to leave the area.

No fish were caught within a 3-hour period after 2030, indicating that they scatter to feed some distance away from their daytime haunts, perhaps as far as adjacent sandy areas as described by Hiatt and Strasburg (1960). Few if any sounds were recorded from the area after the school had left and until it returned shortly before dawn, although the fish did produce sounds at night when confined in aquaria. Nocturnal activity of laboratory populations was similar to that of fish in the field, i.e., they began to swim more actively out of the cave and showed color changes typical of specimens caught by hook and line at night. The period of nocturnal feeding corresponded to the time of greatest locomotory activity by isolated fish in the activity chamber, as was the case with *H. rufus* (Winn et al., 1964).

Differences in behavior between *H. rufus* and *M. berndti* were observed in (1) the types of sounds produced and in their diel distribution, (2) responses of laboratory populations to sound playbacks, and (3) movements in the field. It is possible to explain these differences by comparing their nonreproductive social organization.

Individuals of *H. rufus* are territorial, but fish may maintain territories a few meters apart and certainly within acoustic range. These fish produce at least three different types of sounds: hand-held sounds, which presumably communicate the presence of a predator by a captured fish; staccatos, emitted by individuals when startled or when a predator approaches; and grunts, produced during territorial defense, especially involving intraspecific aggression but also the chasing of a nonpredatory fish of another species from the territory. Display behavior, involving fin erection, nipping, shuddering, and lateral displays are additional components of territorial defense. "Mobbing" may occur, at least under laboratory conditions, when a predator swims through closely spaced territories of a number of fish. Winn et al. (1964) have pointed out the similarity between elements of the acoustical system of *H. rufus* and certain behavior patterns of birds which roost together though maintaining territories, and which will mob a predator, show crepuscular peaks of sound production, and have analogous behavioral responses to alarm calls. The acous-

tical system of *H. rufus* aids in maintaining territories by individual fish and also promotes the survival of all fish in adjacent areas with a warning call. The peaks in production of staccato sounds at dawn and dusk are believed to be the response of territorial squirrelfish to movements of other species through their territories. The initial response of laboratory populations to playbacks of staccato sounds consisted of retreat by each individual into the open can within his territory, followed immediately after the playback by orientation to and investigation of the sound source by a few fish.

The evidence presented here indicates that *M. berndti* is nonterritorial. Fish in the laboratory were never observed to defend particular areas of the cave from others. The presence of large groups of fishes in the field, schooling under broad ledges or inside open caves, supports the contention that menpachi live in nonterritorial aggregations during the day. Further evidence was the absence of any aggressive behavior or associated sound production toward individuals of other species of nonpredatory fishes introduced to populations in the laboratory, or to diurnally active groups of reef fishes frequently observed to enter and leave habitats occupied by menpachi in the field. The presence of appeasement postures, shown by several fish in three populations, could be expected in this type of a social system. Lastly, nocturnal scattering, probably some distance from their daytime haunts, would make territoriality a highly transitory phenomenon.

The most common type of sound produced by menpachi was a series of knocks. It is assumed that these sounds are associated with the chasing of a small fish by a larger one in field populations, because only under these circumstances were the sounds produced in the laboratory. The hypothesis presented here is that, while territoriality promotes spacing of individuals in *H. rufus*, chasing and knock sounds function to maintain distance between individuals in *M. berndti*. This does not mean that some fish would be driven into open water, but that they would tend to space themselves throughout a given cave or ledge area, reducing the danger that more than one individual could be caught by a predator and increasing the likelihood that a predator approaching from

any direction would be detected. Moray eels were prominent potential predators, often seen in pairs or larger aggregations in the same habitat as menpachi.

Growl sounds produced in the laboratory were associated with more intense aggressive interactions. This sound is associated with aggressiveness between pairs of fish both willing to fight. In about half the observed cases these sounds followed nipping between the two fish. When one of the two fish fled, knocks were produced by the attacking fish and, possibly, also by the fleeing fish.

In three of the four field recordings, there was no evidence of a crepuscular peak in the production of staccato and grunt sounds. In one recording, a dusk peak occurred (April 28–29). This was the only case when the hydrophone cable was not secured near the surface with an air-filled bottle. Movements of the loose cable on the bottom under the ledge, combined with decreased light intensities, may have been responsible for the production of these sounds.

The response of laboratory populations to moray eels consisted of orientation to the eel's head, investigation of its tail, increase in rate of swimming movements, and the production of many grunt and a few staccato sounds. The response of natural populations to a diver was similar acoustically, but the fish had room to escape by scattering to either side or back into darker recesses. More staccato sounds were produced by laboratory populations during the first few seconds after the eel appeared, while grunts were produced throughout the 1-minute recording period, though at a decreasing rate as time passed and the eel made no further movement after entering the cave. Apparently the tendency to produce grunt sounds habituates at a slower rate than staccatos. Probably staccatos represent the most intense warning response to danger stimuli. These sounds were also occasionally produced by startled menpachi during introductions of nonpredatory fish which suddenly entered the cave.

Sound-playback experiments to four laboratory populations indicated that fish responded differently to various types of their own sounds. There was no observable change in the behavior of fish during playbacks of background

sounds. Some fish oriented to the speaker when knocking sounds were played back, but did not move to the sound source. The response to playbacks of both staccato and grunt sounds involved immediate orientation, followed by movements toward the sound source. Playbacks of staccato sounds suppressed activity in *H. rufus*, i.e., the fish retreated into their cans during the playback, as would be expected when the territory also included a protective area. Orientation to the sound source occurred just outside the can and, in some cases, the fish moved toward and investigated the experimental speaker after the sound had been turned off. These differences in responses by both species to their warning sounds can be attributed to territoriality in *H. rufus* and its absence in menpachi. In both cases it is clear that *M. berndti*, and probably *H. rufus*, are capable of orienting to a sound source located a few meters away, and that staccatos (and grunts in menpachi) warn that a predator is present and also indicate his location. A warning sound with no directional information would be of limited use when large numbers of fish are aggregated in areas of low light intensity, probably not alone sufficient to permit visual localization of a well camouflaged predator. Presumably, the responses in the laboratory are made to the "near field" components of the sounds, since they occur within a meter of the source. The results support van Bergeijk's (1964) contention that fishes are capable of localizing sounds within the near field. It would seem that *M. berndti*, which shows such clear responses to some playbacks, would be a good species to test for sound localization at greater distances in the far field.

Reproductive activities in fish have led to the evolution of one or, usually, two distinct types of sounds. One of these, usually produced by males, presumably attracts and/or sexually stimulates the female. Some examples are the "boat-whistles" of toadfish (Gray and Winn, 1961; Winn, 1964), "purrs" of *Notropis analostanus* (Stout, 1963), and the sounds of male *Bathygobius soporator* and *Chasmodes bosquianus* (Tavolga, 1956, 1958). The same sound may function in aggressive interactions between males during the breeding season, as in the cod (Brawn, 1961), but often a second

sound is used in nest defence or male-male fighting, for example the "knocks" of *N. analostanus*, and grunts and growls of toadfish and midshipman (Gray and Winn, 1961; Cohen and Winn, in preparation). In *M. berndti*, an acoustical system involving the production of at least five types of sounds, including the hand-held grunt, has been evolved. These sounds are correlated with nonreproductive behavior patterns. Other sounds may be used during spawning, but to date no information is available. It may be supposed that the development of increasingly complex acoustical systems (more distinct types of sounds correlated with specific behaviors or with different intensities of one behavior pattern) will occur when large numbers of fishes aggregate throughout the year, at least for certain periods of the day. Such aggregations promote a variety of intraspecific contacts in different behavioral contexts and increase problems of vulnerability to predators. This explanation might account for two types of sounds associated with different intensities of aggressive behavior (knocks and growls) and warning (staccatos and grunts) in *M. berndti*. There have been few studies to date, but it is interesting that several (3-5) types of sounds have been recorded from nonreproductive groups of squirrelfishes and aggregations of marine catfishes (Tavolga, 1960).

Winn (1964) has proposed that fish sounds may be categorized into five basic types: variable interval, fixed interval, unit duration, time-length, and harmonic-frequency signals. Intermediates are not uncommon. He has suggested that information could be transmitted by varying the intervals as well as the unit lengths, although there are cases when these variables do not seem to be involved. Differences in intervals and duration of units appear to differentiate sounds produced by menpachi, although there are also some minor differences in frequency and intensity between various sounds. Since *M. berndti* responds preferentially to some of its own signals, it might be possible to test these variables with artificial sound playbacks. It is assumed that all types of sounds in these fish are produced by different temporal patterning of contractions by the same pair of muscles associated with the air bladder.

The squirrelfish are well suited for bio-

acoustical studies because they will produce sounds and can usually be kept under semi-natural conditions in the laboratory for observations and experiments. At least two other species in the Hawaiian area (*Holocentrus xantherythrus* and *H. lacteoguttatus*) produce different sounds in intraspecific aggressive behavior and warning (Salmon, unpublished observations). While *H. xantherythrus* was found in groups under ledges and in caves, *H. lacteoguttatus* appeared to be territorial. It appears that quite different types of social organization and patterning of sounds may be characteristic of each species of squirrelfish. Further studies on other species may yield valuable information on the evolutionary development of acoustical communication in the Holocentridae, and in marine fishes in general.

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